LEAF LITTER DECOMPOSITION IN HAWAIIAN STREAMS

AUTHORS

KELLY M. ARCHER
HAWAII COOPERATIVE FISHERY RESEARCH UNIT
UNIVERSITY OF HAWAII
2538 THE MALL
HONOLULU, HI 96822

NOW: BOX 428 C/O HAWAII PREPARATORY ACADEMY
KAMUELA, HI 96743

AND

JAMES D. PARRISH
HAWAII COOPERATIVE FISHERY RESEARCH UNIT
UNIVERSITY OF HAWAII
2538 THE MALL
HONOLULU, HI 96822

INTRODUCTION

Research in temperate streams has demonstrated the importance of terrestrially produced organic material as an energy source (Cummins 1974; Boling et al. 1975; Fisher and Likens 1972; Fisher 1973). Small woodland streams in particular may depend to a large degree on allochthonous material (Fisher and Likens 1972; Cummins et al. 1972, 1973; Peterson and Cummins 1974). Because of this dependence on the terrestrial environment, headwater streams are often referred to as heterotrophic systems (Anderson and Sedell 1979; Vannote et al. 1980).

Litter processing in streams in the densely forested watersheds of Hawai'i may provide a principal source of energy for stream life. Drastic flow variations due to orographic and seasonal rainfall may inhibit benthic algal growth. This, coupled with low light conditions due to thick vegetation canopies, reduces in-stream autochthonous production.

Leaf litter constitutes a major percentage of allochthonous input to the headwaters of Hawaiian streams. Large quantities of leaf material in various stages of decomposition can be seen in accumulations on the upstream sides of boulders or other obstructions. Very little work has been done on leaf processing and the invertebrate populations which utilize this material in tropical or subtropical regions (Padgett 1976). Even less is known about lotic ecosystems in tropical insular environments (Harrison and Rankin 1975). The role of leaf litter in the energy regime of Hawaiian streams has not been determined, but it may well be of overriding importance in the maintenance of the biotic system.

As allochthonous material enters a stream, soluble components are quickly released (1-3 days) through leaching. This process is followed by fungal and bacterial colonization which 'conditions' the leaf surface, creating an attractive substrate for invertebrate species (Triska, Sedell and Buckley 1975; Triska 1970; Suberkropp and Klug 1976). Apparently aquatic hyphomycetes initiate conditioning by breaking down cell surfaces (Triska 1970). Bacteria colonize the fungal hypha and utilize the dissolved organic nutrients released by the hyphomycetes, thus increasing the nutritive value of the leaf as a food substrate. The leaf surface is then more attractive to invertebrate stream organisms such as crustaceans, molluscs and aquatic insect larvae. Predation on these organisms by fish, amphibians, certain crustaceans and insect species extends the influence of allochthonous organic material to other trophic levels.

The objective of this study is to determine the rate of processing and the invertebrate colonization pattern of 3 common riparian leaf species in 2 streams on the island of O'ahu, Hawai'i. Extensive work has been done on temperate streams in detailing the decay rate and the types of invertebrates involved in the processing of allochthonous material. This information makes it possible to comment on the interaction of the terrestrial environment and the stream for maintenance and management purposes. The results of this study may be broadly applicable in Hawai'i and other tropical insular regions and may serve as an important tool in efforts to preserve threatened lotic environments.

MATERIALS AND METHODS

Study Sites

Two streams on the island of O'ahu were selected for this study (Figure 1). Preliminary work was done in April and May 1981 in Kaaawa Stream, windward O'ahu. The main portion of the study, February-May 1982, utilized Waihi tributary of Manoa Stream, leeward O'ahu.

Kaaawa Stream originates at about 100 m elevation and drains an area of approximately 10.3 km^2 which consists principally of steeply sloping ridges and a narrow valley floor. Stream discharge is generally low and varies greatly with rainfall. The study site is located mid-valley at 40 m elevation approximately 2 km inland. Mean stream depth is 0.2 m, width 1.5 m, and water temperature range was 20-23 C during the study period. The substrate is composed principally of cobble with small patches of sand. Riparian vegetation includes guava (*Psidium guajava*), hau (*Hibiscus tiliaceous*) and smaller herbaceous species. Low light conditions resulting from this vegetative canopy prevent conspicuous algal growth. The elevation gradient of the study site is approximately 7-10 %. Leaf litter and other allochthonous material is generally present, forming natural accumulations of various sizes. The aquatic fauna includes native and exotic species and is characteristic of the few relatively unaltered streams remaining on O'ahu.

The principal study site is located in Waihi tributary in upper Manoa valley. This leeward stream drains an area of 2.95 km^2 and is located northeast of the University of Hawaii campus and a residential area. Waihi originates at 940 m elevation and joins Waiakeakua tributary forming Manoa Stream, which flows alongside the university campus and eventually into the Ala Wai canal, a large drainage canal adjacent to Waikiki. Much of the main stem of Manoa Stream is channelized for flood control purposes.

The 100-m long study site lies at an elevation of 120 m, below Manoa falls and the park land adjacent to it. Riparian vegetation consists of bamboo (*Bambusia vulgaris*), monkeypod (*Samanea saman*), mango (*Mangifera indica*), hau (*Hibiscus tiliaceous*) and a number of small herbaceous plants. Very low light conditions occur because of the thick canopy.

Mean stream depth in the Waihi study site is 0.3 m and width 3 m. The gradient of the site is approximately 10% and the stream bottom is composed of boulders and cobble. Water temperature ranged from 18 to 20 C during the study period. Large quantities of allochthonous material are present on the upstream side of the boulders and other obstructions in the stream.

The discharge of Waihi stream varied greatly during the study period, as is characteristic of many Hawaiian streams. The mean discharge was 0.24 m^3/s; the range was 0.03 to 2.36 m^3/s (USGS unpublished data).

Leaves

Three leaf species were selected for this study, based upon availablity and their importance as a source of allochthonous material in streams. Hau trees commonly form dense thickets along Hawaiian streams. The hau leaves are often large (e.g., 25 x 20 cm), thin and very pliable. They are easily torn and seem to contain little refractory support tissue. Leaves can easily weigh 2.5 g each when dried to constant weight. The octopus tree (Brassaia actinophylla) produces large (e.g., 25 x 15 cm), fleshy leaflets which have a thick, waxy surface. These leaflets are less fragile than hau leaves yet weigh nearly the same per unit area. Hala leaves (Pandanus odoratissimus) are thick, long, narrow blades (e.g., 10 x 100-120 cm), very rigid and resistant to weathering. These blades were, and to a certain extent still are, used by Hawaiians for weaving baskets and mats and as roof and wall material for thatched huts. The leaf is largely composed of refractory support material, and a single leaf can weigh over 50 g when dried. Hau leaves were used in the Kaaawa study, while hau, octopus and hala leaves were used in Waihi.

Experimental Procedures

Fresh leaves were picked from trees within the watershed and air dried (1 week) to a constant weight. Hala leaves were cut into 15-cm lengths to facilitate pack formation. Following procedures outlined in Peterson and Cummins (1974), leaf packs were formed using plastic "Buttoneer" staples (Dennison Manufacturing Co.). Preliminary work in Kaaawa stream utilized 10-g packs; 5-g packs were used in Waihi stream. In addition, in the Waihi experiment, each pack was placed within a 10 x 15-cm bag made of 2.5-cm square nylon mesh. This step was taken in an effort to prevent the loss of the entire leaf pack during sudden high flow periods. Each leaf pack and bag was stapled to an elastic band (see Merritt et al. 1979). The elastic band was then attached to an anchor brick which was placed in the stream with the broad surface of the leaf pack facing into the current.

A total of thirty-four 10-g hau leaf packs were placed in Kaaawa Stream. Two packs were removed after 48 hours to serve as controls to account for losses due to chemical leaching and handling damage. Four packs were removed on each of 3 subsequent sampling days.

In Waihi stream 150 packs were placed in the stream, 50 of each species. Four packs of each species were removed after 48 hrs to determine breakage/leaching losses, and thereafter 4 randomly selected packs of each species were collected each sampling day.

Packs were removed from the bricks and placed in individual plastic bags. In the laboratory, leaf packs were separated from the nylon bags (Waihi experiment) and rinsed carefully over a tray. The water was then filtered through a 0.15-mm mesh screen. The material retained was hand sorted using a Bausch and Lomb BV 1070 binocular microscope at 20 to 30 magnification. Animals were preserved in alcohol for identification and enumeration. Identification was done using Ward and Whipple (1959) and Merritt and Cummins (1978). The leaf packs were dried at 50 C for 48 hrs, then weighed to the nearest 0.01 g.

Processing rates were determined using a negative exponential model (Peterson and Cummins 1974)

$$W_d = W_o e^{-kd} ,$$

where:

W_o = weight of leaf material at the end of the initial 48-hr leaching period

W_d = weight of leaf material remaining d days after the end of the initial leaching period

and

k = rate coefficient.

Data were fitted to the above model using least squares regression.

RESULTS

Processing Rates

Processing data for each leaf species at Waihi and Kaaawa are given in Table 1. Curves showing per cent leaf weight remaining are given in Figure 2. For purposes of curve fitting, the initial weight, W_o , is the weight at the end of the initial leaching period, i.e. 2 days after placement in the stream. All mention of day number refers to the number of days after the leaching period.

In Waihi Stream hau packs processed at the fastest rate, followed by octopus and then hala. The 10-g hau packs in Kaaawa decomposed at a slower rate than the 5-g hau packs in Waihi. The percentage of weight loss due to leaching in the first 48 hrs ranged from 20 % for hala leaf packs to 13 % for octopus and Kaaawa hau leaf packs .

Some of the mesh bags originally containing hau and octopus leaves in Waihi Stream were empty when collected due to leaf material tearing away from the "Buttoneer" staples, beginning at day 23 of the study. These empty mesh bags were counted in determining the set of 4 to be collected per species but were not used in computing the decay coefficients since these zero values reflected transport of leaf material from the study site and not processing. This procedure resulted in less than 4 inputs to the regression analysis on the last 4 collection days for hau leaves and on 3 of the last 4 days for octopus leaves. In effect this resulted in uneven weighting of importance for those bags which did contain leaves of these species when collected on these days. Table 2 shows the number of packs of each species sampled on each collection day. The hau and octopus portion of the Waihi experiment ended on day 34, while the hala experiment lasted until day 61. The experiment ended for each species when no mesh bag marked for that particular species could be found in the study area.

Invertebrates

Table 3 contains a list of the animals associated with leaf packs during this study. All animal collections were from the Waihi study involving hau, octopus and hala leaf packs. Identifications are to the most specific level possible with confidence. Functional feeding groups listed are modified from Vannote, et al. (1980) and Anderson and Sedell (1979). Of the 5 functional feeding groups described by these authors (predators, shredders, collector-gatherers, filter feeders and scrapers), only the shredder group is not represented in collections during this study.

The total number of individuals of the 5 most common invertebrate taxa per gram dry weight leaf material is shown in Figure 3. Data are expressed as a mean of the samples taken each collection day, for each of the 3 leaf species. Of the 11 animal taxa listed in Table 3, five dominated numerically in all collections. The most abundant taxon was the Subclass Copepoda. The other 4 groups which appeared most frequently were: Chironomidae (midges), Empididae (danceflies), Hydropsychidae (caddisflies) and Oligochaeta (segmented worms). Figures 4, 5, and 6 show the mean numbers of organisms in each of these taxa per gram dry weight leaf material for each of the 3 leaf species.

The copepod and oligochaete taxa were clearly dominant numerically. Both groups tended to steadily increase in number until some apparently critical period was reached, then a dramatic reduction occurred. Three insect families of 2 orders were present in small numbers. Comparison of Figures 4, 5 and 6 with Figure 3 suggests that the decline in total animals per gram on each of the 3 leaf types on day 23 is primarily a result of a sharp decrease in the number of oligochaetes present.

Throughout the study period more insects, especially midges and caddisflies, were found associated with octopus and hau than with hala. No other major difference was apparent, although there were differences between the number and type of animals found on each leaf species.

Although microbial colonization levels were not monitored during this study, observations indicated extensive populations producing substantial quantities of jelly-like slime on the surfaces of leaves incubated in the stream.

DISCUSSION

Natural accumulations of leaf litter in headwater streams in Hawaii are ubiquitous. Lush vegetation contributes litter throughout the year, apparently with no large seasonal variability. Temporal variations in biotic processes attributed to seasonal influences in temperate streams may not occur in lotic environments in Hawaii.

A number of factors are involved in the processing of leaves in streams and jointly determine the rate at which it occurs. Preconditioning in the terrestrial environment, stream temperature, physical abrasion, leaching, microbial colonization and macroinvertebrate feeding all have been associated with leaf degradation (Anderson and Sedell 1979).

Processing Rates

The relative decay coefficient values in Table 1 are not surprising, given the anatomy of the 3 leaf species. Hau leaves are large and quite thin, and rapid processing would be expected. Octopus leaves are also large but have a sturdy, rigid structure. Hala leaves are extremely tough and resist ripping and puncture. Thus the decay coefficients found during this study are consistent with the physical characteristics of each species.

Discharge in Hawaiian streams may vary considerably over short periods of time. Seasonal storms and orographic rainfall increase surface runoff, increasing discharge rapidly. The relatively short, high gradient, direct route from headwater to the ocean, characteristic of most Hawaiian streams, also results in very little lag time between rainfall and freshet conditions. Breakage of leaf litter during high water conditions is a natural phenomenon which probably plays an important part in the processing of leaf material in the Hawaiian lotic environment. The result of the fragmentation of allochthonous material due to turbulent flow may be similar to the particle size reduction effect attributed to stream invertebrates in mainland studies (Cummins 1974, Vannote et al. 1980).

Peterson and Cummins (1974) described mainland leaf groups in terms of decay coefficients. Group I species were considered 'fast' and have decay coefficients greater than 0.010. Group II, 'medium' species, have k values ranging from 0.005 to 0.010. Group III species are 'slow', with coefficients less than 0.005. All 3 leaf species used in this study would be considered 'fast' according to these criteria.

The growing number of leaf processing studies completed in North American temperate streams have produced numerous decay rates to compare with Hawaiian values. Judging from the results of this study and the physical characteristics of the leaves of riparian vegetation in Hawai'i, the processing rates of many Hawaiian species would be considered fast in comparison with mainland rates. Hala, with a half life of 38 days, may well represent the most long-lived leaf material entering Hawaiian streams.

Comparing the results of preliminary work at Kaaawa and the work done at Waihi involves at least 4 considerations. Mesh bags were used at Waihi but not at Kaaawa. There is some evidence that size of bag mesh can affect processing rate (e.g., Benfield et al. 1979). The 2 streams are different in size and flow characteristics. Hart and Howmiller (1975) and Sedell et al. (1975) found that large streams processed leaves more quickly than did small streams. Initial pack size for the Kaaawa trial was twice as great as that for Waihi. Wecker (1979) and Benfield et al. (1979) found that packs with smaller initial weight had higher k values than larger packs of the same leaf species under the same conditions. Hau leaves were used in the studies of both Kaaawa and Waihi streams and permit direct comparisons.

The decay coefficient for hau in Waihi was much higher than in Kaaawa (0.087 and 0.046, respectively). There seems to be no firm basis for assessing the effect of containment by the mesh bags. Greater hydrodynamic stresses and abrasion on the leaf packs in the larger, more turbulent Waihi Stream may have been a major factor in its higher processing rate. The smaller leaf pack size in Waihi may have also contributed to its greater k value.

Invertebrates

An interesting leaf pack colonization pattern is shown in Figure 3. All 3 leaf species show a steady increase in the number of total animals, followed by a swift decline and another increase shortly thereafter. This pattern of 2 invertebrate density peaks has been documented by a number of authors (Peterson and Cummins 1974; Reice 1977; Wecker 1979).

A factor that may have been involved in invertebrate colonization patterns during this study is stream discharge. On the day prior to the day 19 sampling, a winter storm caused a freshet with stream discharge of twice the mean value for the study period. In addition, following day 34 there was a week of high flow, peaking at 4 times mean discharge. This high flow preceded the day 43 collection for hala leaves. Invertebrate densities were found to be lower following high stream discharge days. Flow was below mean discharge values during the time when total animal counts were highest. The invertebrate taxa mainly responsible for high density values were oligochaetes and copepods. These animals would seem to be particularly vulnerable to displacement by high flow velocities and thus especially sensitive to drastic stream flow fluctuations.

Invertebrates associated with decomposing leaves may affect rates of processing (Anderson and Sedell 1979). Emphasis has been placed on the importance of the shredder functional feeding group (Cummins et al. 1973; Barlocher and Kendrick 1975). Many temperate stream studies have shown that after the initial conditioning phase of decomposition, shredder organisms colonize the leaf packs (reviewed in Anderson and Sedell 1979). Substantial leaf weight loss has been attributed to shredders through direct consumption and fragmentation of leaf material. Shredders may increase processing rates by increasing surface area exposed to microbial colonization by their feeding activity (Cummins et al. 1973; Peterson and Cummins 1974). Other studies discount invertebrates as important to leaf degradation. Reice (1977,1978) found no correlation between animal abundance, species richness or species diversity and the rate of decomposition of leaf packs. Mathews and Kowalczewski (1969) stated that invertebrate feeding was not important in leaf decomposition in the River Thames. Anderson and Sedell(1979) stated that an absence of shredder species in the above studies accounts for the observed results. However, in the Colorado and Fraser Rivers, Short and Ward (1980) found lower processing rates in sites with greater shredder populations. The importance of invertebrates in leaf breakdown studies is highly variable.

Hawaiian streams may be considered depauperate in aquatic insects (J.R. Barnes personal communication; F.J. Triska personal communication). The role that aquatic insects play in leaf processing in Hawaiian streams is probably very limited, judging from the low densities of the 3 insect types found in experimental leaf packs.

This study identifies the types of invertebrates associated with leaf litter in Hawaiian streams. No animals known to belong to the shredder functional feeding group were found. Thus the comparatively high decay coefficients must involve factors independent of shredder activity. The community of invertebrates found associated with leaf litter in Hawaiian streams is ecologically diverse, and these animals use the leaf material in diverse ways. The scraper and collector/gatherer functional feeding groups are the most important invertebrates in terms of leaf processing. Their actions expose new surfaces to microbial colonization. Other functional feeding groups appear dependent on leaf litter for habitat. The significance of invertebrate feeding in the breakdown of allochthonous material in Hawaiian streams requires further study, however it seems likely that microbial decay and physical damage due to water turbulence are the important weight loss factors in this study.

System Effects

Fragments produced during leaf processing tend to accumulate in pools or slow reaches of the stream, sometimes producing thick layers of allochthonous material. These accumulations appear rich in microbiota, with anaerobic decomposition often occurring within the thick layer of debris. Strong, periodic freshets serve to scour stream beds, and the fragments are moved further downstream and into the ocean.

The transport of dissolved and particulate organic material downstream may result in an important contribution to the Hawaiian estuarine environment. Nutrients released by leaf litter decomposition probably contribute significantly to the substantial algal productivity that occurs in estuaries, while the particulate matter (often rich in associated microbiota) is directly consumed by certain estuarine organisms (Timbol 1972; Maciolek 1981).

Management implications of detritus in stream ecosystems is a field yet to be seriously explored (Merritt et al. 1979). Studies completed in Hawaii have documented the adverse effects on stream temperature and habitat caused by the removal of riparian vegetation (Timbol and Maciolek 1978; Hathaway 1978; Norton et al. 1978). No attempt has yet been made to assess the affects of addition or removal of detritus in Hawaiian stream ecosystems. Stream clean-up and channelization and a variety of land development activities in the state often reduce the availability of riparian leaf litter as well as reducing the diversity of available habitats and influencing stream biota (Hathaway 1978; Norton et al. 1978). Under these modified conditions the decomposition pathways outlined in this study and the energy and nutrient economy of the stream may be seriously altered.

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TABLE 1. Leaf pack processing data for Kaaawa and Waihi Streams.

STREAM	LEAF SPECIES	EXPOSURE METHOD	INITIAL WEIGHT (g)	NO. OF SAMPLES	TOTAL NO. PACKS	EXPON. DEC.COEF,k (r VALUE)	HALF LIFE,days
KAAAWA	HAU	PACK	10	4	14	0.046 (0.86)	15.0
WAIHI	HAU	PACK IN BAG	5	8	23	0.087 (0.74)	8.0
WAIHI	OCTOPUS	PACK IN BAG	5	8	28	0.050 (0.76)	13.9
WAIHI	HALA	PACK IN BAG	5	11	42	0.018 (0.83)	38.3

Table 2. Number of leaf packs collected for each leaf species on each sampling day, Waihi Stream.

DAYS FOLLOWING 48 hr LEACHING PERIOD	LEAF SPECIES HALA	OCTOPUS	HAU
0	4	4	4
5	4	4	4
13	4	4	5
19	4	4	4
23	4	3	3
27	4	2	1
30	4	4	1
34	4	3	1
43	4	0	0
53	4	0	0
61	2	0	0
Total packs:	42	28	23

TABLE 3. List of invertebrates found associated with leaf packs in Waihi Stream, O'ahu.

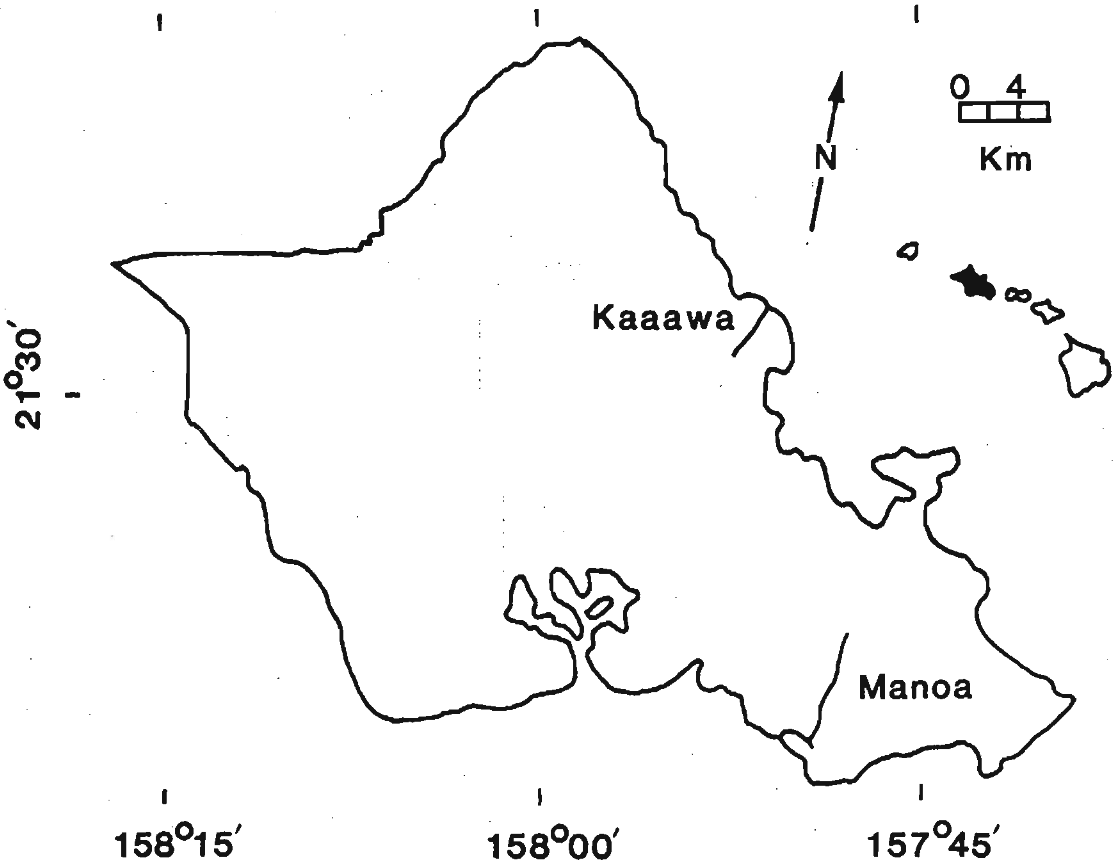
PHYLUM	CLASS	ORDER	SUBORDER	FAMILY	FUNCTIONAL FEEDING GROUPS[a]
ARTHROPODA					
	CRUSTACEA	CALANOIDA			FILTERER[b]
		HARPACTICOIDA			FILTERER[b]
		ISOPODA			COLLECTOR[b]
		AMPHIPODA	GAMMARIDEA		COLLECTOR/ GATHERER; SCRAPER[b]
		DECAPODA	NATANTIA	ATYIDAE (*Atya bisulcata*)	FILTERER; COLLECTOR/ GATHERER[c]
	ARACHNIDA	ACARINA			PREDATOR[b]
	INSECTA	TRICHOPTERA		HYDROPSYCHIDAE (*Cheumatopsyche analis*)	FILTERER[d]
		DIPTERA		CHIRONOMIDAE	COLLECTOR/ GATHERER; FILTERER[d]
				EMPIDIDAE	PREDATOR; COLLECTOR/ GATHERER[d]
MOLLUSCA	GASTROPODA			NERITIDAE (*Neritina granosa*)	SCRAPER[e]
ANNELIDA	CLITELLATA	OLIGOCHAETA			COLLECTOR/ GATHERER[b]

[a]
Predator- preys upon animals associated with leaf packs
Shredder- directly consumes leaf material
Collector/Gatherer- collects or gathers from the sediments, fine and ultrafine particulate organic matter. (FPOM, 50um-1mm; UPOM, 0.5-50um)
Scraper- shears attached algae from surfaces, scrapes or rasps leaf surface for associated biota.
Filterer- filters from transport utilizing specialized structures or constructing nets.

Sources for each particular taxon's assigned feeding group are:

[b] Anderson and Sedell (1979)
[c] Couret (1976)
[d] Merrit and Cummins (1978)
[e] Ford (1979)

Figure 1. Map of O'ahu, Hawai'i showing locations of Kaaawa and Manoa Streams.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Km
Kaaawa
Manoa
21°30′
158°15′
158°00′
157°45′

Figure 2. Per cent dry weight leaf material remaining vs. time for hau leaf packs in Kaaawa Stream and hau, octopus, and hala leaf packs in Waihi Stream. (Values plotted are means of samples. For Waihi hala ± 1 S.D. is shown; this variability is representative of all leaf species. Day number represents days following 48-hr leaching period.)

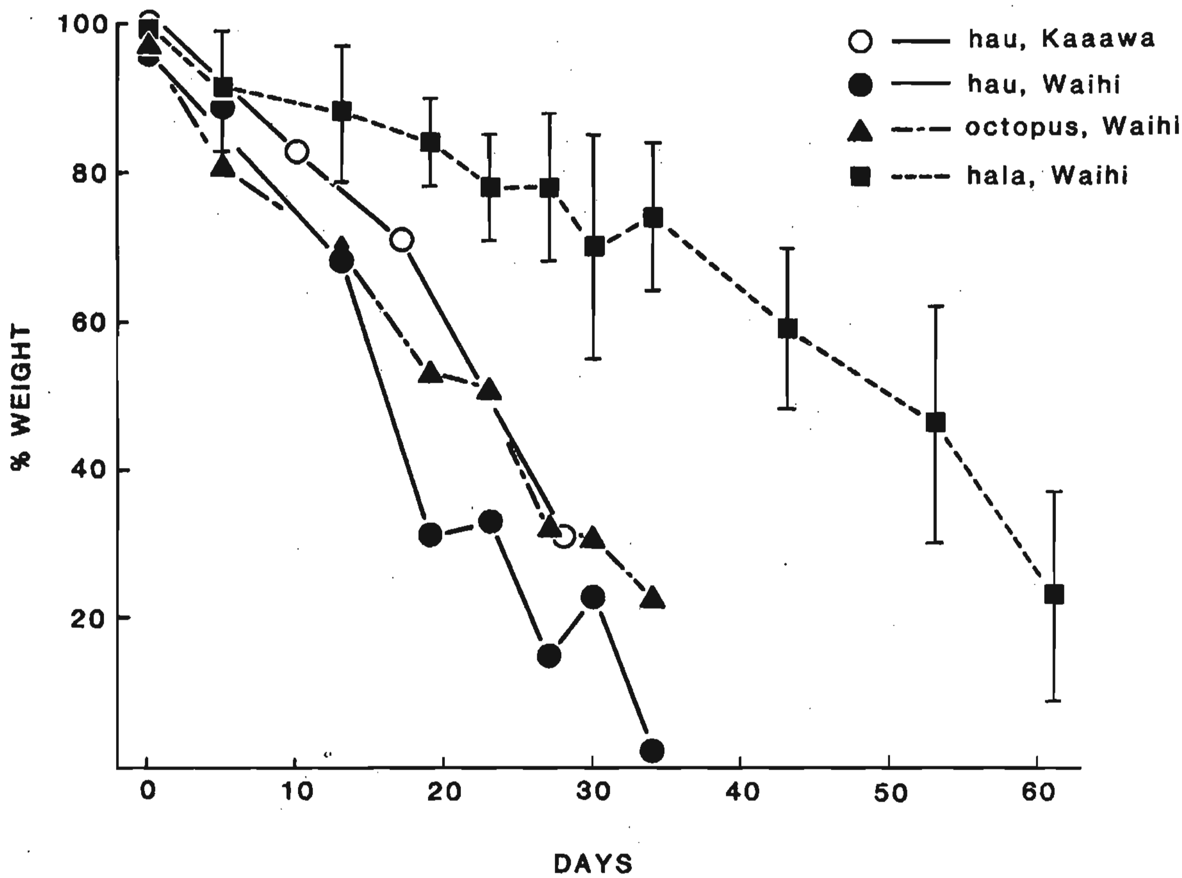

hau, Kaaawa
hau, Waihi
octopus, Waihi
hala, Waihi
100
80
60
40
20
% WEIGHT
0
10
20
30
40
50
60
DAYS

Figure 3. Number of animals per gram dry weight leaf material of the 5 most common invertebrate taxa combined vs. time, for each leaf species. (Each value is the sum of sample means. Day number represents days following 48-hr leaching period.)

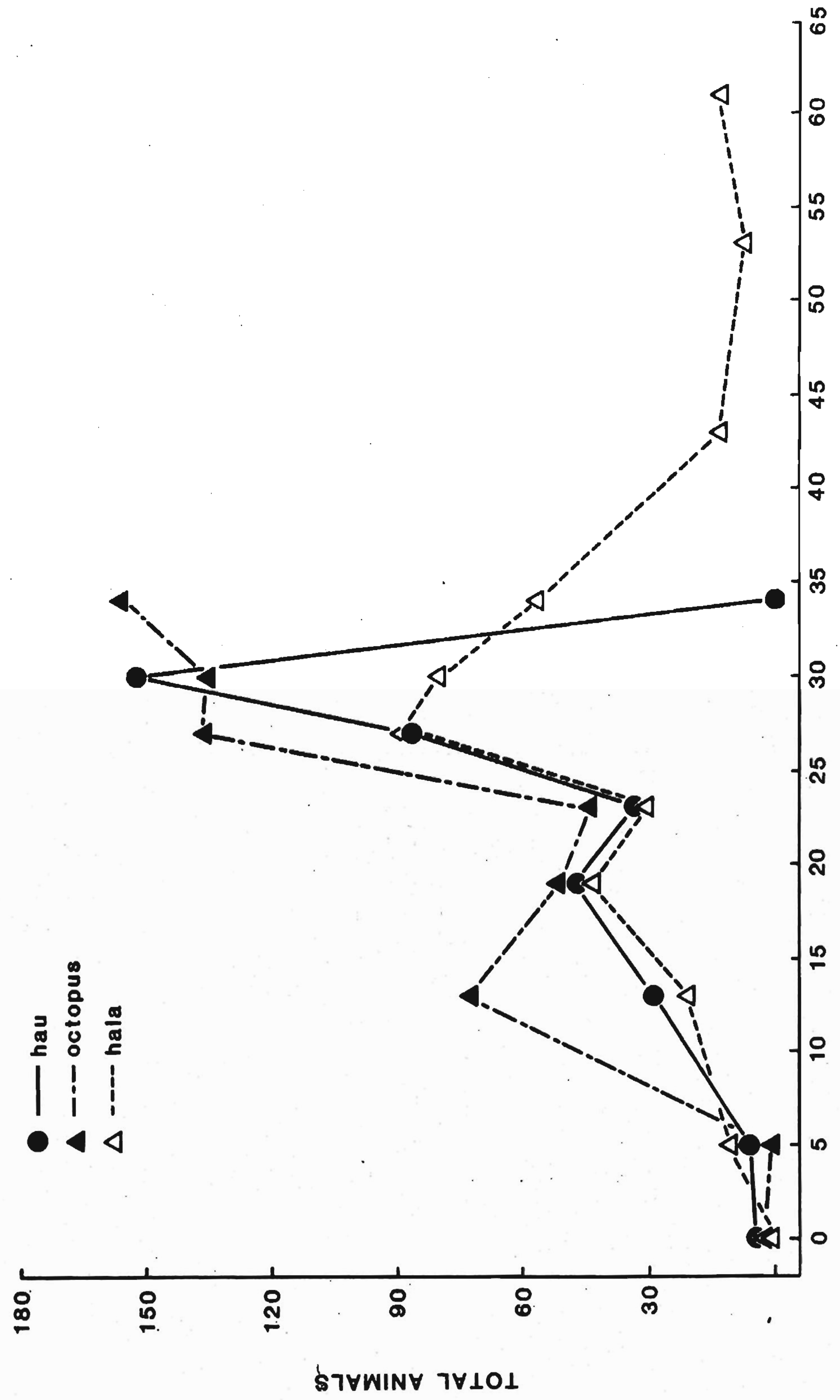

hau
octopus
hala
TOTAL ANIMALS
DAYS
180
150
120
90
60
30
0
5
10
15
20
25
30
35
40
45
50
55
60
65

Figure 4. Number of animals per gram dry weight leaf material of each of the 5 most common invertebrate taxa found on hala leaf packs each sample day. (Each value is the mean for the number of samples shown in parentheses. Day number represents days following 48-hr leaching period.)

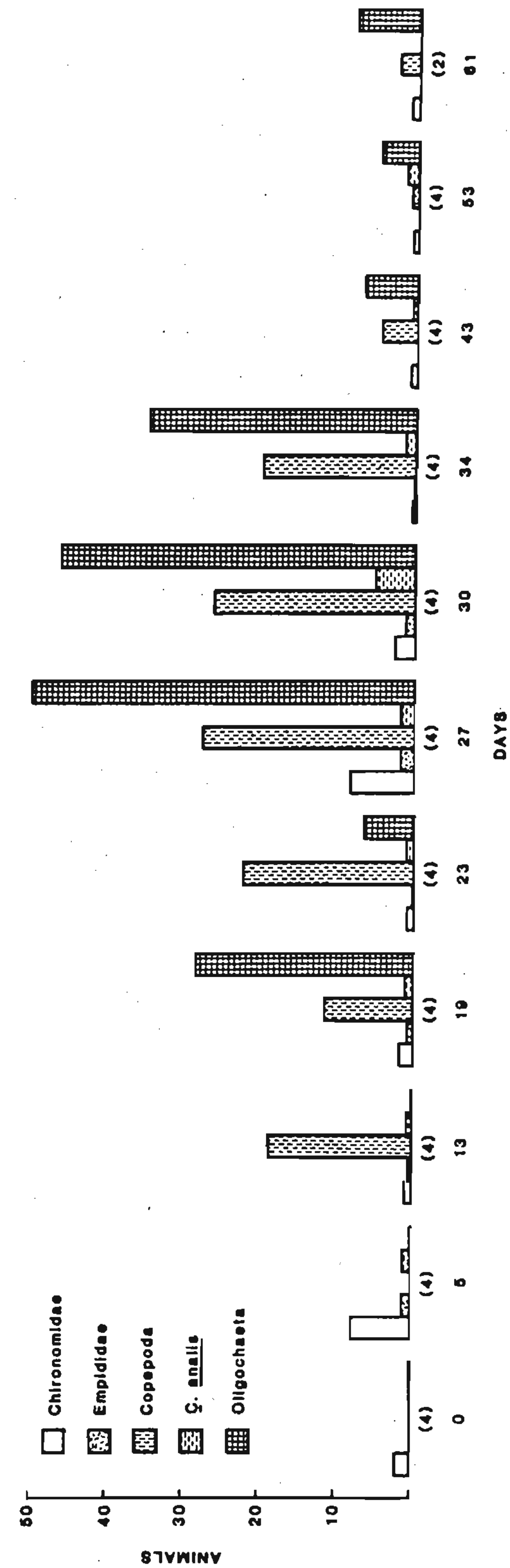
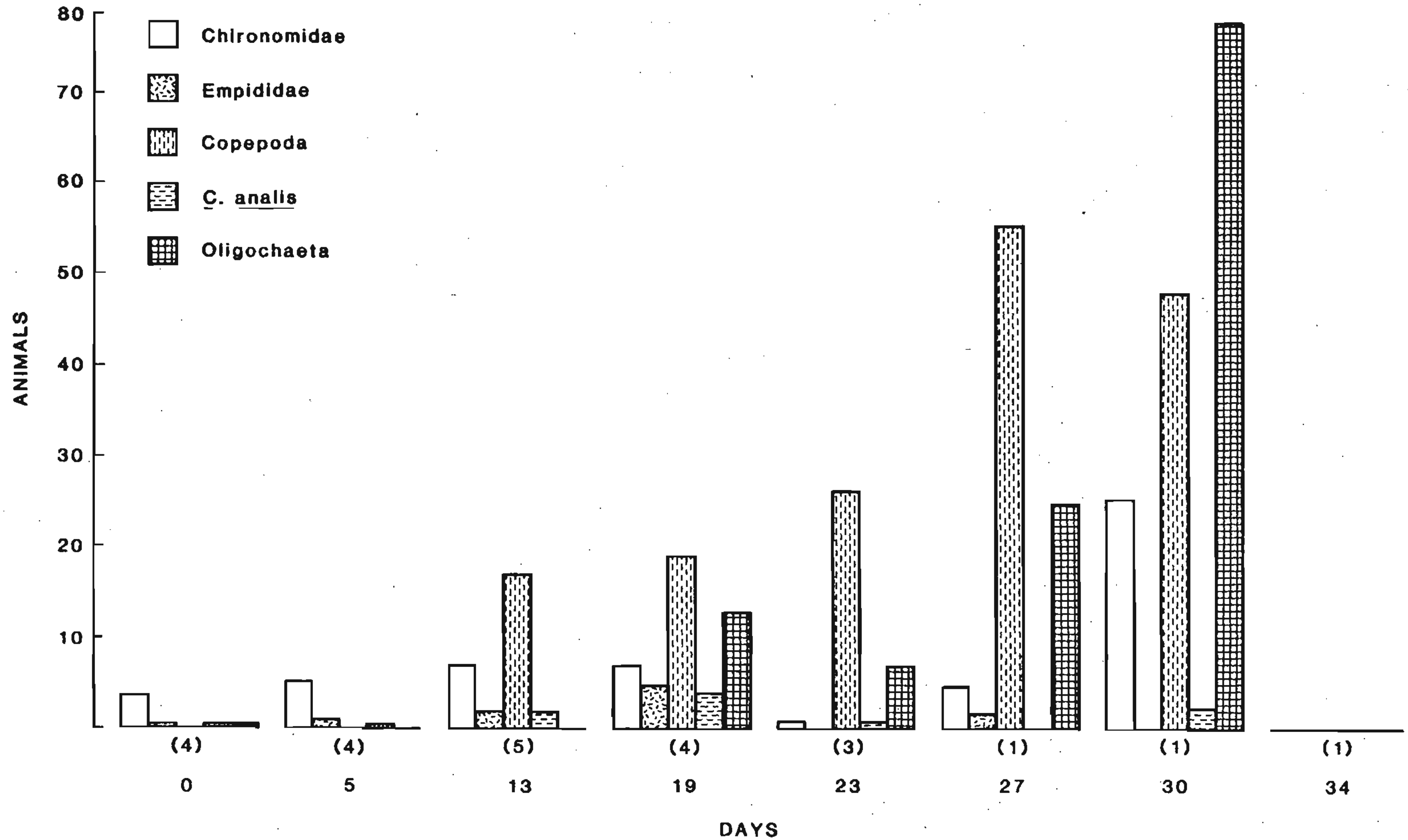
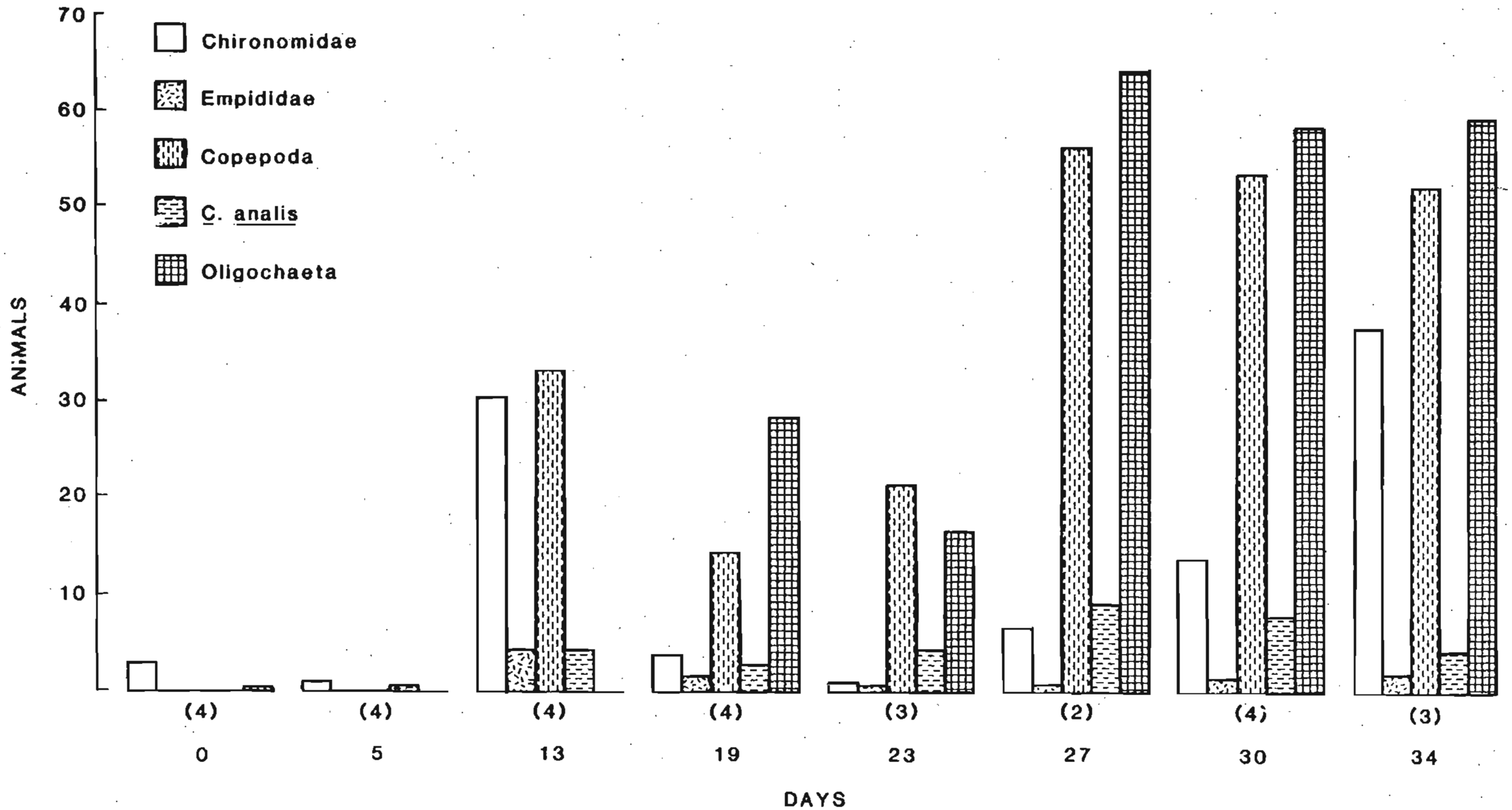

ANIMALS
50
40
30
20
10
DAYS
0
5
13
19
23
27
30
34
43
53
61
(4)
(2)
Chironomidae
Empididae
Copepoda
C. analis
Oligochaeta

Figure 5. Number of animals per gram dry weight leaf material of each of the 5 most common invertebrate taxa found on hau leaf packs each sample day. (Each value is the mean for the number of samples shown in parentheses. Day number represents days following 48-hr leaching period.)



Chironomidae
Empididae
Copepoda
C. analis
Oligochaeta
80
70
60
50
40
30
20
10
ANIMALS
(4)
(4)
(5)
(4)
(3)
(1)
(1)
(1)
0
5
13
19
23
27
30
34
DAYS

Figure 6. Number of animals per gram dry weight leaf material of each of the 5 most common invertebrate taxa found on octopus leaf packs each sample day. (Each value is the mean for the number of samples shown in parentheses. Day number represents days following 48-hr leaching period.)


ANIMALS
70
60
50
40
30
20
10
Chironomidae
Empididae
Copepoda
C. analis
Oligochaeta
(4)
(4)
(4)
(4)
(3)
(2)
(4)
(3)
0
5
13
19
23
27
30
34
DAYS